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Diversification of forest management regimes secures tree microhabitats and bird abundance under climate change

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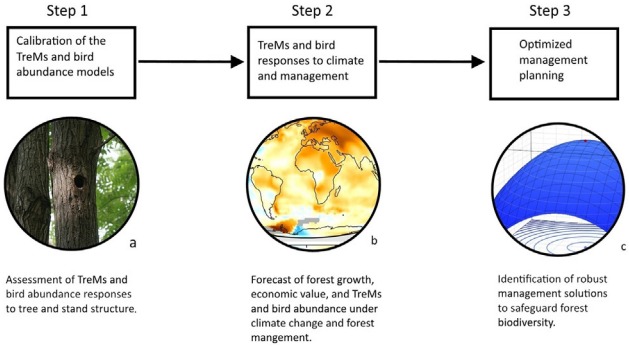
HIGHLIGHTS

- Bird and microhabitat abundance responded to species composition and stand structure.
- Decreased forest management intensity increased microhabitat abundance.
- Avian abundance showed a positive response to increased temperatures.
- Management diversification is required to maintain forest biodiversity in the future.

GRAPHICAL ABSTRACT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ABSTRACT

The loss of biodiversity in temperate forests due to combined effect of climate change and forest management poses a major threat to the functioning of these ecosystems in the future. Climate change is expected to modify ecological processes and amplify disturbances, compromising the provisioning of multiple ecosystem services. Here we investigate the impacts of climate change and forest management on the abundance of tree microhabitats and forest birds as biodiversity proxies, using an integrated modelling approach. To perform our analysis, we calibrated tree microhabitat and bird abundance in a forest landscape in Southwestern Germany, and coupled them with a climate sensitive forest growth model. Our results show generally positive impacts of climate warming and higher harvesting intensity on bird abundance, with up to 30% increase. Conversely, climate change and wood removals above 5% of the standing volume led to a loss of tree microhabitats. A diversified set of management regimes with different harvesting intensities applied in a landscape scale was required to balance this trade-off. For example, to maximize the expected bird abundance (up to 11%) and to avoid tree microhabitat abundance loss of >20% necessitates setting aside 10.2% of the forest area aside and application of harvesting intensities < 10.4% of the standing volume. We conclude that promoting forest structural complexity by diversifying management regimes across the landscape will be key to maintain forest biodiversity in temperate forests under climate change.

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1. Introduction

Forest ecosystem productivity and its multifunctionality are closely linked with underlying biodiversity (Gamfeldt et al., 2013; Ratcliffe et al., 2017). It is therefore of key importance that management schemes strive to maintain sufficient biodiversity levels in forest ecosystems. Changing environmental conditions, however, are predicted to impact the functioning of these ecosystems and influence the effects of conservation practices (e.g. Lindner et al., 2014; Seidl et al., 2017). Therefore, sound conservation actions ask for an integrated analysis of coupled biodiversity and forest responses under climate change. Yet, there is a major gap in the literature for such integrated analyses (Bellard et al., 2012). Here we investigate the interaction between forest structure and biodiversity development under climate change, using tree microhabitats (TreMs) and forest birds as biodiversity indicators, and apply a robust optimization framework to find optimal management schemes to safeguard biodiversity in the future.

Tree microhabitats are "a distinct, well delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrates or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed" (Larrieu et al., 2018). These microhabitats are typical for veteran trees and old-growth forests and have been related to the provision of habitat for several forest taxa of ecosystem services (Michel and Winter, 2009; Paillet et al., 2017). The maintenance of such old-growth attributes for biodiversity conservation, such as TreMs, relates to a large body of the literature dealing with legacy attributes and retention forestry practices proposed during the past 3 decades (e.g. Bauhus et al., 2009; Franklin et al., 1997; Gustafsson et al., 2012; Mitchell and Beese, 2002; Whitman and Hagan, 2003). The maintenance of these old growth elements are crucial to the maintenance of biodiversity, particularly of invertebrates and fungi, and can speed the recovery of ecosystem functioning after disturbances and forest management operations (Franklin, 1989; Simonsson et al., 2015).

The role of habitat trees as 'lifeboats' in the ecosystem has been considered to a certain extent in the scientific literature (e.g. Bütler et al., 2013; Vandekerkhove et al., 2013; Lindenmayer, 2017) and the preservation of this function of trees constitutes an important element of retention forestry (e.g. Fedrowitz et al., 2014; Gustafsson et al., 2012). The abundance of TreMs, provided by living habitat trees is considered a valuable indicator of biodiversity at the stand scale (e.g. Larrieu et al., 2014; Winter and Möller, 2008). TreMs provide substrate and shelter for several taxa and include structural features such as cavities, crown deadwood, mistletoes, cracks and nests, epiphytes, among others (Larrieu et al., 2018; Paillet et al., 2018). The maintenance of the diversity of TreMs in adequate abundance can be regarded as a multi-taxon approach that provides tree-related habitats for various species (Paillet et al., 2018). The use of TreMs to identify and select habitat trees is well established and implemented in management schemes, also for temperate forests (Winter and Möller, 2008; Michel and Winter, 2009; Larrieu and Cabanettes, 2012; Larrieu et al., 2014, 2017; Paillet et al., 2017). However, the development of TreMs on retained trees under different management intensities and climate change scenarios has not been investigated. Additionally, there is a lack of suitable longitudinal data about the temporal development of TreMs on single trees, solely cross-sectional studies have been carried out (Courbaud et al., 2017).

The bird assemblage of forest ecosystems can provide valuable information about habitat quality and is currently widely applied as a biodiversity indicator across Europe (Gao et al., 2015; Gregory and van Strien, 2010). Bird abundance provides valuable insights regarding the structural complexity of forests. The response of birds to structural complexity has been studied since the 60s (e.g. MacArthur and MacArthur, 1961) and theory predicts that the number of species is positively dependent on the resource range, which increases with structural complexity of the canopy of a forest (MacArthur, 1984). Since these early studies, evidence shows a pattern of positive response to forest structural complexity not only of birds, but a wide spectrum of forest taxa as well (e.g. Poulsen, 2002; Roth, 1976; Stein et al., 2014; Tews et al., 2004). Therefore, TreMs and bird assemblage may be regarded as complementary indicators of forest biodiversity, providing valuable information for planning conservation actions. However, long-term assessments of the effect of retention forestry on birds are still lacking (Mikusiński et al., 2018a). The retention of key elements might not be enough to ensure the persistence of forest-specialist bird populations without sound landscape management (Woodley et al., 2006) and long-term planning (Seidl et al., 2014). To understand the influence of forest management and retention forestry on biodiversity, it is necessary to analyze the effects of the future structural changes of forests on birds (Mikusiński et al., 2018a).

The socio-economic context in which forest ecosystems are embedded may affect the success of the implementation of conservation efforts. In this sense, evaluating economic implications of retention practices is warranted, since the maintenance of living habitat trees and deadwood on forest stands will require that managers forego harvesting income from these trees, and thus represents an opportunity cost (Koskela et al., 2007; Rosenkranz et al., 2014). Changes in forest productivity due to climate change are also expected to affect the profitability of timber production (Hanewinkel et al., 2013) and the costs of retention forestry. In order to support conservation practices, we need to evaluate these economic aspects of retention forestry to define sufficient retention levels and adequate compensation for forest owners willing to improve forest habitat quality. Moreover, as different taxa may have different habitat requirements (e.g. Mönkkönen et al., 2014), it may be necessary to create management schemes that balance multiple objectives in forest landscapes.

The aim of this study was to identify impacts of forest management and climate change on forest biodiversity in temperate forests using TreMs and birds' abundance as complementary biodiversity indicators, and to find suitable forest management solutions to safeguard the maintenance of biodiversity in forest landscapes. Hence, the main research questions were:

1) What are the relevant forest characteristics to promote the abundance of TreMs and the abundance of birds?
2) How do climate change and forest management scenarios influence the provisioning of TreMs and bird abundance in the future? and
3) What are robust conservation solutions for the maintenance of TreMs and bird abundance in managed temperate forests under climate uncertainty?

To answer our research questions, we used field data from 139 plots to parametrize the response of TreMs and bird abundance to tree and stand structure. These statistical models were then applied in a simulation-optimization framework to forecast the abundance of forest birds and TreMs in a temperate forest landscape in Southwestern Germany. We considered nine different climate change scenarios and eight forest management regimes with varying harvesting intensity. To find management solutions to maintain forest biodiversity, we used a robust optimization scheme, by maximizing the abundance of birds under climate uncertainty and constraining TreMs loss.

2. Material and methods

2.1. Study area

The empirical data for forest structure, TreMs and birds were obtained from 139 one-hectare plots for TreMs in a study area in southwest Germany in the Black Forest (latitude: 47.6°–48.3° N, longitude: 7.7°–8.6° E; WGS 84). The selection of plots followed two gradients. At the landscape scale there was a forest cover gradient represented by three categories (<50%, 50–75% and >75%) of forest cover in a 25 km^2 circular area centered in the plot centers, with a minimum distance between plots of 1 km. At the forest stand scale, the second selection

criteria was the number of standing dead trees identified by photo stereo viewer technique representing a gradient from 0 to >20 dead trees per hectare. The plots represent a typical temperate mixed mountain forest, dominated by Norway spruce (*Picea abies* (L.) Karst.), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*), located at altitudes between 500 and 1400 m a.s.l. All plots were located on publicly owned forest land (i.e., excluding roads, buildings and water bodies), and are managed in a continuous cover forestry system, applying thinning from above.

2.2. Forest inventory data

Owing to limited bird abundance data availability, we used a subset of the forest inventory data from 73 research plots, where both bird abundance and TreMs abundance were collected. These plots were embedded in forest landscapes with a forest cover ranging from 20 to 92% in a 25 km^2 circular area (except one outlier displaying a 3% forest cover). We conducted our simulations only for plots where bird abundance information was available, in order to avoid the use of the bird abundance model in areas that did not inform the parameter estimation. Forest inventory data comprised tree species identity and diameter at breast height (DBH) of all living trees (with DBH > 7 cm) and the height of 7% of the trees. The measured heights were then used to fit a logarithmic DBH-height model for each species. These models were employed to predict the height of each tree in the plot. In addition, the DBH and height of all snags on the plots was measured and classified according to its origin as conifers or broadleaved trees. The forest type (pure coniferous, mixed coniferous, mixed-coniferous-broadleaved) as well as different silvicultural treatments (even-aged, uneven-aged, a mix of these two, strict protection) was extracted from forest inventory data provided by the State Forest Administration.

2.3. Microhabitat data

The empirical data for modelling TreMs abundance were collected in the Black Forest on the full set of 139 plots. Since our goal was to apply the model to a variety of climate and management scenarios, we used the full dataset covering a wider range of forest conditions to increase the robustness of our analysis. In total, 2621 living trees were inventoried in the field for TreMs, DBH, location and tree species. The DBH ranged from 20 cm up to >100 cm. It covered a variety of tree species, but the dominating species were Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) accounting for >80% of the inventoried individuals. The mean abundance was 2.4 TreMs per tree. We used a detailed catalogue for TreMs classification by Kraus et al. (2016) which is very similar to a recently published classification system (Larrieu et al., 2018) (Table 1).

Table 1
Types and distribution of tree microhabitats (TreM) in our dataset (6267 TreMs = 100%).

TreM type	Distribution (% of total abundance)
Woodpecker cavities	0.6%
Trunk mold cavities	1.0%
Branch holes	6.6%
Dendrotelms	2.0%
Insect galleries	0.1%
Bark loss	7.1%
Exposed heartwood	0.7%
Cracks and scars	0.5%
Bark	2.7%
Dead branches and crown deadwood	6.6%
Root buttress cavities	40.1%
Witch's broom	1.3%
Cankers and sundburrs	0.7%
Fungi fruiting bodies	0.2%
Epiphytic crypto phanerogams	18.4%
Nests	0.7%
Sap and resin run	10.5%
Microsoil	0.4%

TreMs were recorded for two sample populations of living trees. The first pool of trees comprised the 15 largest individuals in each plot. To identify these trees, the crowns of all living trees per plot were delineated horizontally using the TreeVis software (Weinacker et al., 2004). The relationship between crown size and DBH is well known for the studied tree species (Jucker et al., 2017). The 15 trees per ha with the largest crown sizes were recorded on all 139 plots, yielding 2085 trees. In addition, trees with smaller crown sizes were inventoried on a random subset of 89 out of the 139 plots. We recorded trees with smaller crown areas in three categories (0–31 m^2, 31–58 m^2 and 58–97 m^2). We identified the categories in QGis based on Jenks natural breaks over all tree crowns (Jenks, 1967). This sample group consisted of 536 trees.

2.4. Bird abundance data

The bird data were collected using a standardized point count protocol from 73 plots that were surveyed three times during spring 2017, starting half an hour after sunrise with the latest end at 12:00 CET. A single survey lasted 20 min and consisted of four 5-minute-blocks, during which every bird heard or seen was recorded. The surveys were carried out from the plot center and all the birds recorded outside of a 50 m radius were excluded from the analysis. Since the data collection was restrained to one season, we extended the length of the bird point counts, compared to the classical 10 or 5 minute counts (Fuller and Langslow, 1984). It has been shown that 10 minute point counts, repeated twice in the season, can provide a good assessment of the actual bird community (Sorace et al., 2000). Moreover, 3 sampling session can lead to a sample coverage beyond 90% in forests (Balestrieri et al., 2017). We tested our assumption of reasonably surveying the whole community by estimating the completeness of the sample collection using rarefaction/extrapolation curves (Chao and Jost, 2012). We estimated the sample coverage for every plot by using the R package 'iNEXT' (Hsieh et al., 2016) (details in Supplementary 3). The final data consisted of a matrix Species × Session for each plot, as in the following example:

Plot z	Session 1	Session 2	Session 3
Species 1	$x_{1,1}$	$x_{1,2}$	$x_{1,3}$
Species 2	$x_{1,2}$	$x_{2,2}$	$x_{2,3}$
…	…	…	…
Species n	$x_{n,1}$	$x_{n,2}$	$x_{n,3}$

where x is the number of individuals encountered in the plot z. We followed the definition of 'forest bird' and 'forest specialist bird' as in Mikusiński et al. (2018b).

The design variables (number of snags and forest cover) were used only to ensure that plot selection covered a large variation in stand and landscape conditions. Subsequently, a full inventory was done for every plot in order to characterize them with continuous variables, in terms of the stand structure and site conditions (basal area, altitude, slope, among others). Therefore, we did not test the effect of the design variables in our model but relied on the finer inventory data. In this sense, plot selection followed the unique study design but the data regarding the forest inventory, microhabitats and birds were collected and modelled independently.

2.5. Statistical analysis and forest growth under climate change

To perform our analysis, we applied a novel integrated model approach in a three-step analysis (Fig. 1). We used field data to parametrize the response of our biodiversity indicators (TreMs and bird abundance) to tree and stand characteristics. These models were subsequently coupled with a climate sensitive forest growth model. The coupled model was applied to quantify changes in the abundance of TreMs and forest birds in relation to different management regimes and climate change scenarios. Finally, we considered the responses of

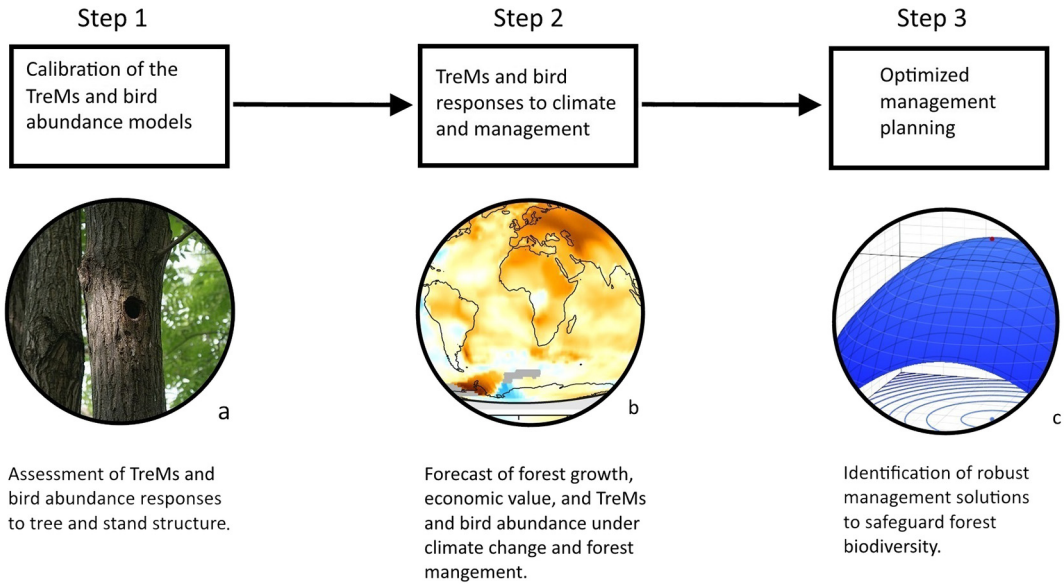
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Fig. 1. Steps performed in our analysis. TreMs stands for tree microhabitat.
Sources: https://commons.wikimedia.org/wiki/File:Tree_hollow_in_Sevastopolsky_park.JPG[a], https://commons.wikimedia.org/wiki/File:Global_Warming_Map.jpg[b], https://commons.wikimedia.org/wiki/Category:Optimization#/media/File:MaximumParaboloid.png[c].

our management regimes to realize the optimal forest management portfolio for our research area.

2.5.1. Model for microhabitats

To model the abundance of microhabitats per tree we used a generalized linear mixed model (GLMM) with fixed and random effects (Eq. (1)). Due to the fact that the trees are located within the same plots we included the plot as random effect to prevent spatial autocorrelation (Legendre, 1993). The other variables included as fixed effects were DBH, tree species, altitude of the individual tree, and the two design gradients, forest cover in the surrounding landscape as well as the number of standing dead trees in the plot. Several of these variables such as DBH, tree species, management, forest type and standing dead wood have been tested for their influence on TreMs before (Vuidot et al., 2011; Larrieu and Cabanettes, 2012; Paillet et al., 2017). Additionally, altitude represents a climate-sensitive site indicator, which is essential for further climate change scenario modelling and the forest cover in the surrounding landscape might influence the abundance of TreMs due to abiotic and biotic processes that create them.

$$\begin{aligned} MicroHabitatPerTree = \; & \exp(b_0 + b_1 Altitude + b_2 Species + b_3 DBH \\ & + b_4 ForestType + b_5 ForestCoverCategory \\ & + b_6 SilviculturalSystem + b_7 Snags + b_8(1|PlotID) \end{aligned} \quad (1)$$

where:

Species = tree species,
DBH = diameter at 1.3 m,
ForestType = forest type,
ForesCoverCategory = forest cover in the surrounding landscape (%),
SilviculturalSystem = management system applied,
Altitude = tree altitude (m a.s.l.),
Snags = number of snags ($N \cdot ha^{-1}$).

The modelling was carried out in R (RStudio Team, 2016) using the lme4 package (Bates et al., 2014). We tested the significance of the predictors on the abundance of TreMs for prediction purposes under climate change. Moreover, since our predictors could present collinearity, e.g. altitude and tree species, we assessed the variance inflation factors between our predictors.

2.5.2. Bird abundance model

The model for birds focused on estimating the abundance of every species and provided an estimate for the abundance of the full assemblage. In this way we were able to have information about the community, while not losing single species responses. The use of abundance data is usually preferred to presence-absence data, as they include more information (Howard et al., 2014). Bird abundance was estimated using a community N-mixture model that retained the full species identity (Kéry and Royle, 2015). The model consisted of N-mixture models (Royle, 2004) applied for each recorded species by employing hierarchical modelling. Such model can also adjust the estimates for imperfect detections. The community process, i.e. if the species k belongs to the community at site i or not was modelled as a Bernoulli process: $a_{i,k} \sim \text{Bernoulli}(k)$. The species abundance models were dependent on the community process and were modelled using a Poisson distribution: $N_{i,k} \sim \text{Poisson}(a_{i,k} * lambda_{i,k})$. Finally, the detectability was accounted for, by employing a binomial observation model: $y_{i,k,j} \sim \text{Binomial}(N_{i,k} * p_{i,k,j})$, which assumes that a species can be recorded only if present at the site (i.e. it is depended on the abundance model).

An early data-inspection revealed a skewed distribution of the counts, suggesting the use of a zero-inflated Poisson model for estimating abundance. Species heterogeneity was included by modelling both abundance and detectability as a function of the predictors. The data from the forest inventory and the estimated abundance of TreMs were used to predict abundance, while the date and time were used for adjusting the detectability. Considering the data requirements, we could include the bird data from 73 plots in the model. The full model (Eq. (2)) was built in JAGS language and fitted applying Bayesian inference. We used uninformative priors and running three chains 180,000 iterations, discarding the first 90,000 and thinning by 90. We considered that chains reached convergence when the Gelman-Rubin statistic was ≤1.1 for all parameters. The analysis was conducted in R environment,

using the package 'jagsUI' (Kellner, 2017). The R-hat value was used to examine Markov chain convergence (Gelman and Hill, 2007).

$$\lambda i = \phi_i \exp(b_{0i} + b_{1i}Slope + b_{2i}Altitude + b_{3i}BA + b_{4i}ConiferShare + b_{5i}VolDead + b_{6i}NDead + b_{7i}TMHA) \quad (2)$$

where:

λ_i = abundance of species I,
ϕ_i = zero inflation coefficient,
Slope = average plot slope (°),
Altitude = plot altitude (m a.s.l.),
BA = plot basal area ($m^2 \cdot ha^{-1}$),
ConiferShare = share of conifers (%),
VolDead = volume of lying deadwood ($m^3 \cdot ha^{-1}$),
NDead = number of snags ($N \cdot ha^{-1}$),
TMHA = total tree microhabitat abundance in the plot ($TreMs \cdot ha^{-1}$).

2.5.3. Forest growth model

Forest development was assessed with the distance-dependent forest growth model Sibyla (Fabrika, 2007). Sibyla simulates the growth of each tree in forest stands based on potential height and diameter increments (Hlásny et al., 2011), subsequently adjusting the actual growth according to environmental factors, competition and tree vitality. The model is climate sensitive and applies growth potential reduction factors according to soil characteristics (moisture and nutrient content) and climatic conditions, including: atmospheric CO_2 and NO_2 concentration, length of vegetation season, temperature amplitude, average temperature during growing season and precipitation sum during the growing season (Fabrika et al., 2018). Sibyla is capable of simulating different management concepts and deriving economic parameters of forest management, such as assortment structure and harvesting revenues.

For the model initialization, we used the forest inventory data of our research plots, including the DBH, tree species and estimated height for the trees that were not directly measured. The tree coordinates in the plots were automatically generated by the model applying the STRUGEN stand generator (Pretzsch, 1997). We simulated forest development over a 50-year period with management interventions every 10 years and eight management scenarios to analyze the impacts of forest management on the development of the habitat trees and associated TreMs. We considered eight management regimes applying thinning from above with increasing intensity, removing 0, 2.5, 5, 7.5, 10, 12.5, 15 and 17.5% of the standing volume (S1-Table 1 – see Supplementary material 1). We point out here that these management interventions simulated a selection harvesting system for mature stands with large average DBH. To account for climate change impacts on forest development, TreMs development, and bird abundance we assessed the results of each management regime under nine different climate change scenarios (Table 2). Climate change scenarios were obtained as a combination of three General Circulation Models (GCM) and three Representative Concentration Pathways (RCP), bias corrected by ISI-MIP. We selected RCP 4.5, 6.0 and 8.5 with forecasted temperature increase close to recent central estimates and policy pledges (Cox et al., 2018).

To forecast the development of TreMs and bird abundance under climate change, we coupled the results of our forest growth model for all 72 scenarios (8 management regimes and 9 climate change scenarios), with the TreMs and bird abundance models. We kept the share of conifers constant (at the mean value) for the bird abundance model, since broadleaved-dominated stands are largely underrepresented and we did not consider tree species conversion in our management alternatives. Moreover, we assessed the economic impacts in terms of the net present value of the stand applying a 1.5% interest rate. Taking into account that altitude is a proxy for climatic conditions, we corrected the altitude for the TreMs and bird abundance forecasts. We assumed that each degree increase in temperature under climate change caused a 188.7 m altitude reduction in our plots, according to the lapse rate estimated in the region (Paul, 1976).

Table 2
Climate change scenarios as a combination of a Global Circulation Model (GCM) and Representative Concentration Pathway (RCP). Temperature change and the precipitation refer to the period 2017–2066.

Climate scenario	GCM	RCP	Temperature change (°C)	Precipitation (mm)[a]
1	HadGEM2-ES	4.5	2.8	559
2	IPSL-CM5A-LR	4.5	1.2	649
3	NORESM1-M	4.5	1.1	611
4	HadGEM2-ES	6.0	2.0	685
5	IPSL-CM5A-LR	6.0	2.1	589
6	NORESM1-M	6.0	2.0	586
7	HadGEM2-ES	8.5	3.3	613
8	IPSL-CM5A-LR	8.5	2.3	634
9	NORESM1-M	8.5	2.3	615

[a] Precipitation during vegetation season.

2.5.4. Robust conservation model

The maintenance of biodiversity is crucial for ecosystem functioning and service provisioning under climate change. Climate development, however, is largely uncertain (Yousefpour and Hanewinkel, 2016) and conservation planning needs to include this uncertainty in order to safeguard the provisioning of suitable forest structure including TreMs for promoting biodiversity. We performed a robust conservation planning, in order to maximize bird abundance under climate uncertainty, while maintaining TreMs abundance at desirable levels. In this sense, we aimed to find a management portfolio that was robust (stable across all climate change scenarios) towards climate change uncertainty. Moreover, we constrained the TreMs maintenance between 10 and 100% of the observed abundance at the beginning of the simulation period, establishing a trade-off frontier between bird and TreMs abundance. To select the optimal forest management portfolio to safeguard the forest bird abundance under climate change uncertainty (details in Supplementary 2), we applied a bridged Bernstein-CVaR approximation scheme (Ben-Tal et al., 2009).

3. Results

3.1. Model for microhabitats

Our results show that increasing DBH as well as increasing altitude led to an increase in TreMs abundance per tree (Table 3). Tree species identity had a significant influence on TreMs abundance, where silver fir, Douglas fir (*Pseudotsuga menziesii*), Scots pine (*Pinus sylvestris*) and larch (*Larix decidua*) displayed on average lower TreMs abundance than Norway spruce. Conversely, broadleaved species, namely beech (*Fagus sylvatica*), sycamore maple (*Acer pseudoplatanus*) and Norway maple (*Acer platanoides*) displayed higher TreMs abundance than conifers. Broadleaved species with low frequency and forest cover at landscape scale were not significant predictors for TreMs. Since some of our predictors could present collinearity, we assessed the variance inflator factors among the predictors and obtained VIF below 2 (for the correlation matrix see Supplementary 3 S3-Table 1). Thus, we could use the model to predict overall TreMs abundance per stand as a sum of estimated microhabitat abundance per tree.

3.2. Bird abundance model

The bird data collection returned a list of 55 species and 2542 encounters. Mean sample coverage was 0.837 (Supplementary 3 S3-Fig. 1). Our hierarchical model showed a consistent negative influence of slope, the share of conifers and TreMs abundance on the bird abundance

across all bird species recorded in our dataset (Fig. 2). The bird abundance was especially sensitive to the share of conifers in the plots, the altitude, and TreMs abundance. The surprising negative influence of TreMs abundance on birds, however, was smaller for forest specialists. The abundance of birds decreased strongly with increasing share of conifers (Fig. 2). With increasing altitude the abundance of most species declined (Fig. 2), particularly of those nesting or feeding on the ground. Also aerial feeders showed a decline in density with increasing altitude. Conversely, species mainly influenced by resource availability instead of climate, such as canopy or cavity nesters, showed variable responses to altitude. The number of snags, as expected, had a positive influence on bird abundance, whereas increasing lying deadwood volume generally reduced bird abundance. We highlight here that these two variables together with the basal area of the stand had a small influence on the total abundance of birds compared to the slope, altitude and share of conifers. Forest specialist birds showed patterns similar to the full assemblage to the stand structure variables, but not always consistent patterns were observed among them (Fig. 2). Altitude affected forest specialist bird in different ways, with common crossbil (*Loxia curvirostra*) showing the strongest positive effect. Closely related species such as firecrest (*Regulus ignicapilla*) and goldcrest (*R. regulus*) showed contrasting trends, being negatively and positively affected, respectively. Forest specialists declined with increasing share of conifers in the plots, although common crossbil, nutcracker (*Nucifraga caryocatactes*) and goldcrest showed positive responses.

3.3. Climate change and management impacts

In our simulations, forest management had a dominant impact on the development of TreMs abundance in the plots (Fig. 3). The current average TreMs abundance is estimated at 400 TreMs·ha^{-1} and depending on the climate and management, it may increase by up to 20% compared to the abundance at the beginning of the simulation period. In general, a harvesting intensity above 2.5% of the standing volume in every 10-year period led to a loss of TreMs at the end of the 50-year simulation period. As management regimes with higher harvesting intensities removed more trees from the stand, there was a proportional loss in the predicted TreMs abundance in the forest. The impacts of the projected climate change on TreMs abundance were less pronounced than forest management effects. As expected, TreMs increased in scenarios with decreased removals and reduced forest mortality (e.g. RCP 4.5).

The economic value of the stand in terms of the net present value (NPV) (Fig. 3) increased in scenarios with higher harvesting rates. The increase in harvested volume had a beneficial impact on the economic value of the forest, as it was possible to anticipate harvesting revenues and promote the capitalization of the forest through increased tree dimensions and improvement of the assortment structure of the plot. Climate had an important contribution to profitability and the NPV was highest under RCP 6.0 (on average of all management regimes). In scenarios in which the increase in atmospheric CO_2 was accompanied by an increase in temperature and decreased precipitation led to a lower NPV.

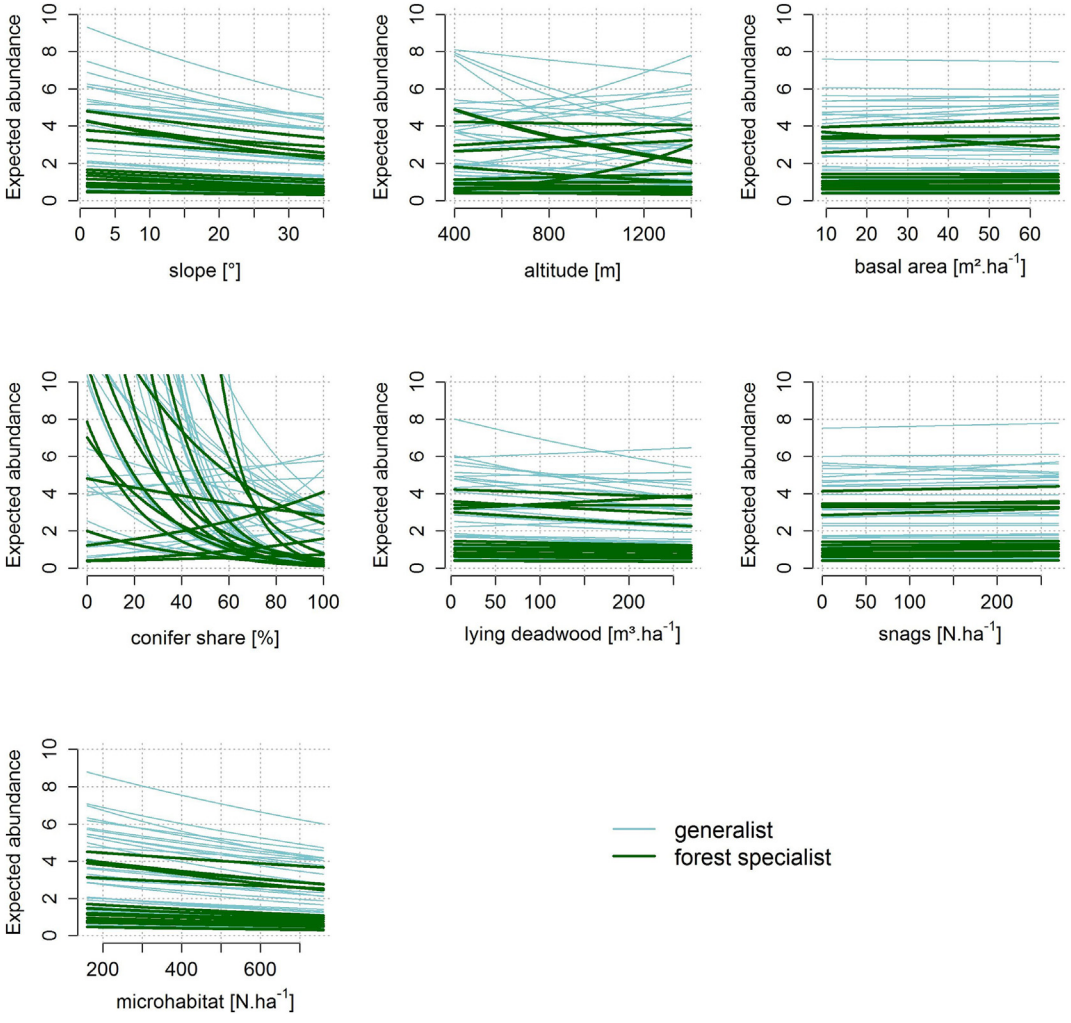

Fig. 2. Response of bird abundance to the habitat variables tested. Forest specialists are depicted in green.

Table 3
Microhabitat model results. The coefficients refer to the fitted tree microhabitat model.

Predictor	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	−1.3E+00*	1.8E−01	−7.177	0.000
Altitude	5.4E−04*	1.9E−04	2.757	0.006
Abies alba	−1.6E−01*	5.4E−02	−2.920	0.004
Pseudotsuga menziesii	−1.0E+00*	1.3E−01	−8.094	0.000
Pinus sylvestris	−2.7E−01*	9.0E−02	−3.007	0.003
Larix decidua	−5.0E−01*	1.8E−01	−2.741	0.006
Quercus petraea	4.0E−01	2.1E−01	1.900	0.057
Fagus sylvatica	4.2E−01*	5.4E−02	7.776	0.000
Acer pseudoplatanus	3.8E−01*	1.1E−01	3.421	0.001
Acer platanoides	9.6E−01*	4.7E−01	2.052	0.040
Fraxinus excelsior	−2.4E−01	1.9E−01	−1.270	0.204
Tilia cordata	−1.3E−01	5.1E−01	−0.266	0.790
Alnus glutinosa	−2.6E−01	6.4E−01	−0.405	0.685
Betula sp.	−3.8E−01	6.3E−01	−0.606	0.545
Salix sp.	4.1E−01	4.9E−01	0.830	0.407
DBH	2.7E−02*	1.1E−03	23.812	0.000
Mixed stand	−2.8E−02	1.1E−01	−0.255	0.799
Strict protection	−8.0E−02	1.8E−01	−0.456	0.648
Uneven aged	−8.3E−02	1.0E−01	−0.801	0.423
Snags	1.5E−03	6.2E−03	0.241	0.810
Coniferous-broadleaved	1.3E−01	7.4E−02	1.699	0.089
Pure coniferous	3.3E−01*	1.6E−01	2.142	0.032
Forest cover 1	2.6E−02	8.1E−02	0.316	0.752
Forest cover 2	1.7E−01	8.8E−02	1.930	0.054

* Significant at 0.05.

The average initial avian abundance in our plots was 167 birds·ha^{-1}. We perceived an overall increase in bird abundance in the next 50 years irrespective of climate trajectory and management intensity (Fig. 4). In the most favorable scenarios it may increase by >20% compared to current levels. Similar to the NPV responses, management regimes applying the most intensive harvesting (17.5% volume removal) displayed the best outcomes for the abundance of birds. Climate trajectories with increased productivity or increased temperature showed higher bird abundance, e.g. for RCP 8.5. These results followed the sensitivity of the bird abundance response to altitude. We observed that the abundance range was narrow for RCP6.0, since all three GCMs had a similar temperature increase under this emission scenario. The right panel in Fig. 4 shows the abundance of the indicators species used in the German Biodiversity Strategy. This forest biodiversity indicator is computed based on the abundance of 10 forest bird indicator species, in comparison with their abundance in the 1970s (a detailed description of the biodiversity indicators has been provided by Dröschmeister and Sukopp, 2009). We observed that, while the general patterns of the bird assemblage and the indicators were similar, the indicator species appear to provide slightly higher figures, compared to the whole assemblage (1% higher increase in abundance overall).

3.4. Robust conservation planning

Intensive management interventions were most frequently applied for maximizing bird abundance in our solution (Figs. 5 and 6). Fig. 5 shows the optimal solution for the most frequent forest type in the study area (mixed conifer-broadleaf forests) and for 80% of TreMs maintenance. We perceived that while the two most intensive management regimes were dominant (17.1 and 21.5% of the total area), there was a strong diversification of the management portfolio. The average harvesting across all management regimes for this forest type was 10.7% of the standing stock and a set aside area of 9.3%.

The average harvesting intensity was sensitive to the TreMs maintenance requirement (Fig. 6). The average harvesting intensity was 15.5% of the standing volume with a large proportion of the most intensive management applied (17.5% of the standing volume) when no TreMs maintenance was enforced (Fig. 6a). With increasing requirement for TreMs, it was necessary to apply less intensive management interventions and for an 80% TreMs maintenance, the average harvesting intensity across all plots decreased to 10.4%, with 10.2% of the plot area set aside, i.e. where no management interventions were applied (Fig. 6b). If no TreMs loss was allowed (Fig. 6c), a strong reduction in wood utilization (to 5% of the standing stock) was necessary.

We observed a synergy between bird abundance and the economic outcome. In contrast, both bird abundance and forest profitability showed a trade-off with TreMs abundance (Fig. 7). Fig. 7a shows the sensitivity of bird abundance to increasing levels of TreMs abundance. Up to a level of 50% of TreMs maintenance there was no change in the optimal management. From 60% to 100% of TreMs maintenance there was a reduction in average bird abundance from 191 to 173 individuals·ha^{-1}. The plot NPV (Fig. 7c) accompanied the same patterns, since the bird abundance responded positively to a basal area and tree number reduction, and therefore higher harvesting levels. However, there was a sharp decrease in NPV, especially for maintenance levels above 60% of the initial conditions, displaying a NPV reduction from 2347 EUR·ha^{-1} to −1634 EUR·ha^{-1}. The loss in microhabitat abundance was reduced from 146 TreMs·ha^{-1} to 0 TreMs·ha^{-1} with the increase in maintenance requirement (Fig. 7b).

4. Discussion

Our modelling indicated that the two biodiversity indicators used in our analysis, tree related microhabitats and birds, responded very differently to different levels of simulated harvesting. While the abundance of TreMs declined with increasing harvesting rates, the abundance of birds actually increased in the simulated 50 years of forest management. Moreover, the effects of different climate change trajectories were less pronounced in comparison to the influence of different management scenarios. We found that forest profitability increased in scenarios with more intensive harvestings and increased forest productivity. Therefore, there was only a limited trade-off between forest profitability and bird abundance maximization in our simulations.

4.1. Microhabitat model

The number of TreMs was positively related to DBH and altitude. The increase in TreMs abundance and richness with increasing tree dimensions has been observed also in other studies and for the same tree species (e.g. Asbeck et al., 2018; Großmann et al., 2018; Michel and Winter, 2009; Winter and Möller, 2008; Vuidot et al., 2011). The increase in TreMs with tree dimension can be partially attributed to tree age, which is a determining factor for the development of TreMs (Michel and Winter, 2009). Since we could not ascertain tree age in the uneven-aged forest in our study, we were unable to further investigate the relationship of TreMs with age. Given the similar growing conditions across the study plots we assume that tree dimension is an appropriate proxy for the physiological tree age. In general, the lack of information on the age-TreMs relationship is acknowledged in science, as so far solely cross-sectional studies (Courbaud et al., 2017) have been carried out in contrast to time series.

We found that broadleaved trees, namely beech, sycamore maple and Norway maple provided a higher TreMs abundance, while silver fir and Douglas fir provided a lower number of TreMs compared to Norway spruce. Larrieu and Cabanettes (2012) report similar patterns for TreMs in montane beech and mixed-fir forests in the French Pyrenees wherein 70% of beech trees provided TreMs but silver fir only 18%. The influence of altitude on TreMs abundance in temperate forest ecosystems has not been closely investigated (e.g. Johann and Schaich, 2016). While the altitude of the plots had a significant influence, we can only speculate about the underlying reasons. These may comprise variations in abiotic processes as duration of and thickness of snow cover, increasing disturbance frequency (such as windthrow and breaking of branches) that create different types of TreMs.

Considering the higher TreMs abundance in broadleaved species, increasing the share of broadleaves in conifer-dominated forests may be a

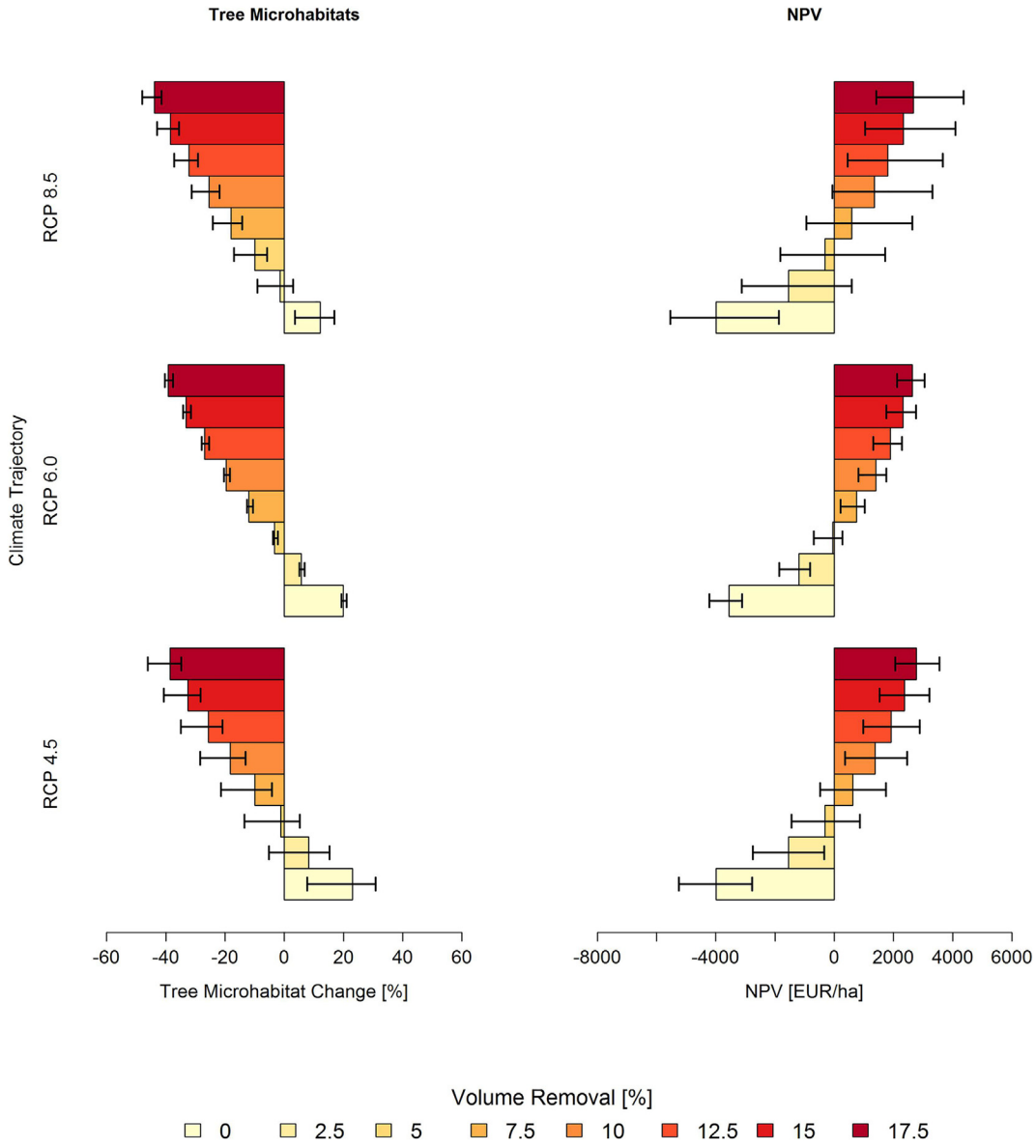

Fig. 3. Average changes in tree microhabitat abundance and net present value (NPV) at the end of the 50-year simulation period. The error bars show the range of tree microhabitats and NPV across the Global Circulation Models tested. The microhabitat change displays the difference in abundance using the first simulation year as basis (400 TreMs·ha^{-1} = 100%) and the volume removal refers to the harvesting amount related to standing volume at each management intervention.

suitable option for increasing TreMs abundance in the future. This can play an important role in the resilience of forest ecosystems, since several TreMs are predicted to buffer climate extremes for some taxa and reduce species mortality under climate change (Scheffers et al., 2014). In our study, TreMs functioned as indicators of structural continuity of forest ecosystem (sensu Groven et al., 2002). Their increase with average tree dimension and age suggests that extending the production cycle length of managed stands or retaining some trees to become veteran or habitat trees will assist the restoration of some old-growth characteristics (Bauhus et al., 2009).

4.2. Bird abundance model

Most of our results for the bird abundance model agree with earlier studies. As expected, the number of snags displayed a positive influence on the total abundance. Snags provide nesting, foraging and roosting habitat for several species (Hutto, 2006), especially cavity-nesters including woodpeckers (Drapeau et al., 2009). The bird abundance also benefitted from an increasing share of broadleaves in forest stands. Abundance and species richness of birds are typically higher in mixed and broadleaved-dominated forests (Felton et al., 2010). Forest birds presented mixed responses to plot basal area, depending on the species considered, with abundant species declining with increasing basal area. Paillet et al. (2010) conducted a meta-analysis on the impact of management on different forest-dwelling taxa in Europe and report that response of the bird assemblage was heterogeneous and other factors, such as the landscape context could explain this variation.

Surprisingly, the abundance of TreMs was negative related to bird abundance. Previous studies had reported a positive influence of TreMs on forest birds (e.g. Laiolo et al., 2004; Regnery et al., 2013), although these results were usually related to specific TreMs or to the diversity of TreMs in the stands (Paillet et al., 2018). We highlight here that the most abundant TreMs in our research area were root buttress cavities (40%), whereas woodpecker cavities were rare (1%). Thus increasing overall TreMs abundance in our study system may not benefit the abundance of birds, in particular not those species reliant on tree hollows. Other reasons for the negative response of bird abundance to TreMs abundance may be related to the contrasting effects of altitude

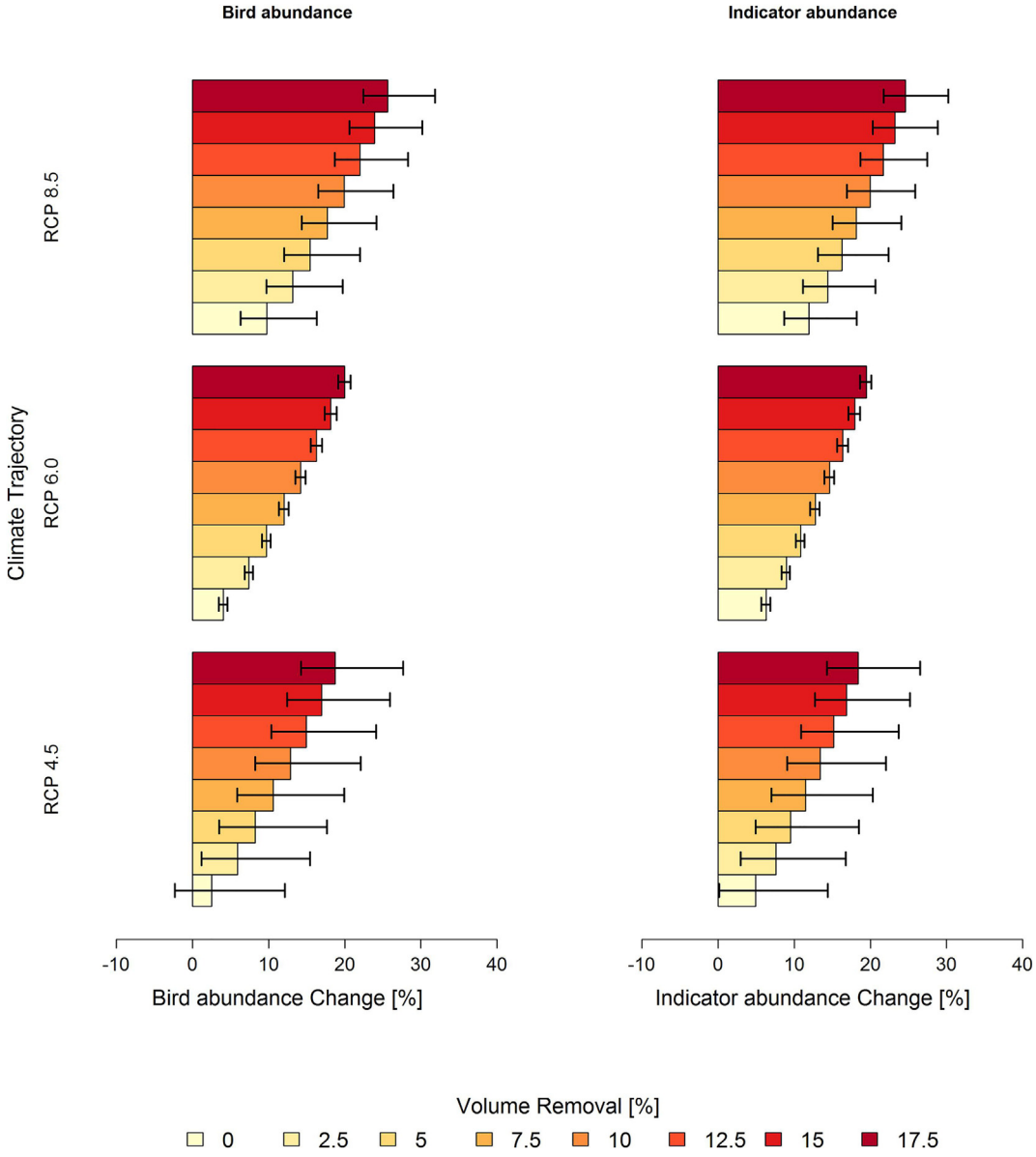

Fig. 4. Average changes of the total bird abundance and of a set of indicator bird species at the end of the simulation period. The error bars show the range of total bird abundance and indicator abundance changes across the Global Circulation Models tested. The change in bird abundance displays the difference in abundance using the first simulation year as basis (167 individuals·ha^{-1} = 100%) the volume removal refers to the harvesting amount related to standing volume at each management intervention.

and stand density on TreMs and bird abundance. High stand densities are typical for conifer dominated stands and these showed reduced bird abundance compared to broadleaf-dominated stands. Moreover, increased stand density resulted in higher basal area, which had a negative influence on bird abundance in our model. In continuous forestry system, the selective removal of trees is increasing spatial heterogeneity of the ecosystem by creating gaps and also initiates fine-scale succession of light demanding plant species suppressed by dark conditions and lower temperature of dense forest. Such local, early successional stages support high productivity of leaves and herbivorous insects e.g. aphids or larvae of lepidopterans leading in turn to higher densities of insectivorous bird (Keller et al., 2003). Fuller (2000) found more species and higher abundances of birds in gaps created by fallen trees in primeval Białowieża Forest in comparison to nearby located forest without gaps. Insectivorous blackcap (*Sylvia atricapilla*) and chiffchaff (*Phylloscopus collybita*) were strongly more abundant in gaps. Also Forsman et al. (2010) found in their meta-analysis of effects of small-scale creation of gaps through harvesting on birds, that bird diversity and abundance was higher in the gaps than in contiguous forests.

Our results also showed that retention of snags and broadleaved trees (similar to TreMs) are effective retention actions to support the bird assemblage in temperate forests. The creation of small canopy openings through harvesting enhanced bird abundance effectively mimicking natural disturbances and increasing habitat heterogeneity of stands (Goetz et al., 2007). The positive influence of broadleaved trees is in line with management recommendations that promote structural complexity in forest stands and increased naturalness in these forests by increasing the proportion of European beech (e.g. Schuler et al., 2017; Yousefpour et al., 2010).

4.3. Climate change and management impacts

In our simulations, management had a dominant influence on future changes in TreMs abundance. Since tree harvesting removes TreMs in standing trees, TreMs abundance decreased with harvesting intensity. This effect was not compensated by the positive influence of harvesting on DBH increment of remaining trees. At the end of the simulation period (50 years), <15% of the trees had a DBH above 70 cm, even for the

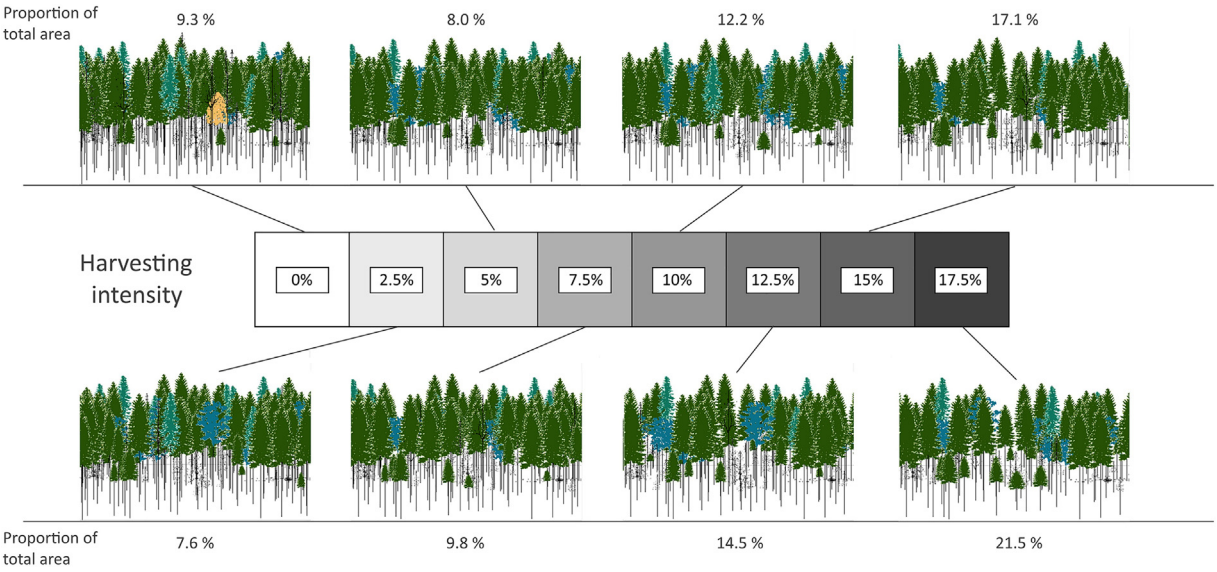

Fig. 5. The figure shows the final state of a typical stand after a 50-year simulation period for the dominant forest type in the study area (mixed conifer-broadleaf forests), and the proportion of each harvesting intensity (0 to 17.5%) applied in the optimal solution considering 80% of microhabitat maintenance. The proportion of total area shows the share of each management regime applied on average across all plots of the same forest type.

most productive scenarios. Yet, in temperate forests, the number of TreMs increases significantly when tree dimensions exceed 68–72 cm DBH (Larrieu et al., 2012). Therefore, owing to the relatively small initial DBH of our plots this positive impact of tree dimensions was not noticeable. With longer simulation periods this effect might increase substantially.

Climate change also played an important role on the development of TreMs abundance, mainly due to changes in forest productivity. It was necessary to harvest a larger number of trees to meet the harvesting targets in the most productive scenarios, compared to less productive ones, leading to a loss of TreMs abundance. Furthermore, this loss was intensified by the increase in temperature for the most extreme scenarios. Since we corrected the altitude of the plots according to the predicted temperature increase in our climate scenarios, and that altitude was positively related to TreMs abundance, climate change led to a loss of TreMs. One can also expect that the increased productivity may cause a reduction in rotation lengths and increase in early harvestings, limiting TreMs development. Conversely, increased forest productivity and density-dependent mortality, under constant harvesting intensity might increase TreMs development. It is important to mention here the role of salvage logging on the provisioning of TreMs abundance under climate and disturbance risk. The removal of dead trees may compromise the provisioning of TreMs in forest stands. The impact of salvage logging on forest biodiversity has recently received more attention. For example, Thorn et al. (2018) conducted a meta-analysis on the impacts of salvage logging on 24 species groups and report a negative influence on saproxylic communities, whereas open-habitat species were positively related to this management action.

The commercial value of the plots increased for management regimes with more intensive wood removals, as it was possible to increase harvesting revenues earlier in the simulation period. Increased forest productivity under climate change was an important driver of forest profitability. In cases where temperature and precipitation were not limiting, higher forest growth rates resulted in increased NPV. Several studies report positive impacts of increasing atmospheric CO_2 on forest productivity (e.g. Reyer et al., 2014; Devaraju et al., 2016). Nevertheless, the extent and persistence of CO_2 fertilization effects is still subject to considerable uncertainty (Kim et al., 2017; Reyer et al., 2014). These positive impacts of climate change on productivity, however, do not take into account possible shifts in species range. Hanewinkel et al. (2013) showed that the change in species distribution ranges may cause a substantial economic loss in European forests.

Climate warming contributed to the positive response of forest birds in the future. Out of 53 species recorded, 33 were negatively impacted by altitude. Therefore, the altitude correction for climate warming benefited most species of the bird assemblage and we observed an overall increase in abundance. Stephens et al. (2016) found similar patterns analyzing the abundance of birds in Europe and North America. According to the authors, a considerable share of species is predicted to benefit from increasing temperatures and climatic suitability showed an increasing trend. On the other hand, Gottschalk and Reiners (2015) predicted that future climate change will cause the decline of 19 forest bird species out of 25 in total (6 species increased). They found also that forest conversion from conifers to deciduous species, modulated climate change effects in such a way that it amplified (15 species) or weakened (10 species) the predicted gains and losses of the species' population size due to climate change. Also, modelling of forest-dwelling bird species in subalpine forests indicated that adaptive habitat management (e.g. increasing number of snags or creating gaps) can to some extent buffer the negative effects of climate change (Braunisch et al., 2014). One must consider, however, that the interactions between bird and plant communities may be more complex than we could consider in our study. Habitat suitability may also change as a result of future shifts in plant species range (Matthews et al., 2011). In this regard, coupling plant and species dynamics models could provide more robust information regarding community trends under environmental pressures.

4.4. Robust conservation planning

To achieve a robust optimal solution considering both biodiversity indicators and economic performance it was necessary to diversify the management regimes within the same plot, combining different harvesting intensities. Apart from the contribution of diversification to risk reduction in an economic sense (Knoke et al., 2016; Knoke et al., 2017), it was necessary to balance bird and TreMs abundance. Our average robust harvesting intensity was 10.4% of the standing volume for maximizing bird abundance while constraining TreMs loss to 20%. Taking into account beech and spruce dominated stands, the current average wood removals in the region amount to 16.3% of the standing stock, across all age classes (BWI 3, 2012). Therefore, current harvesting levels

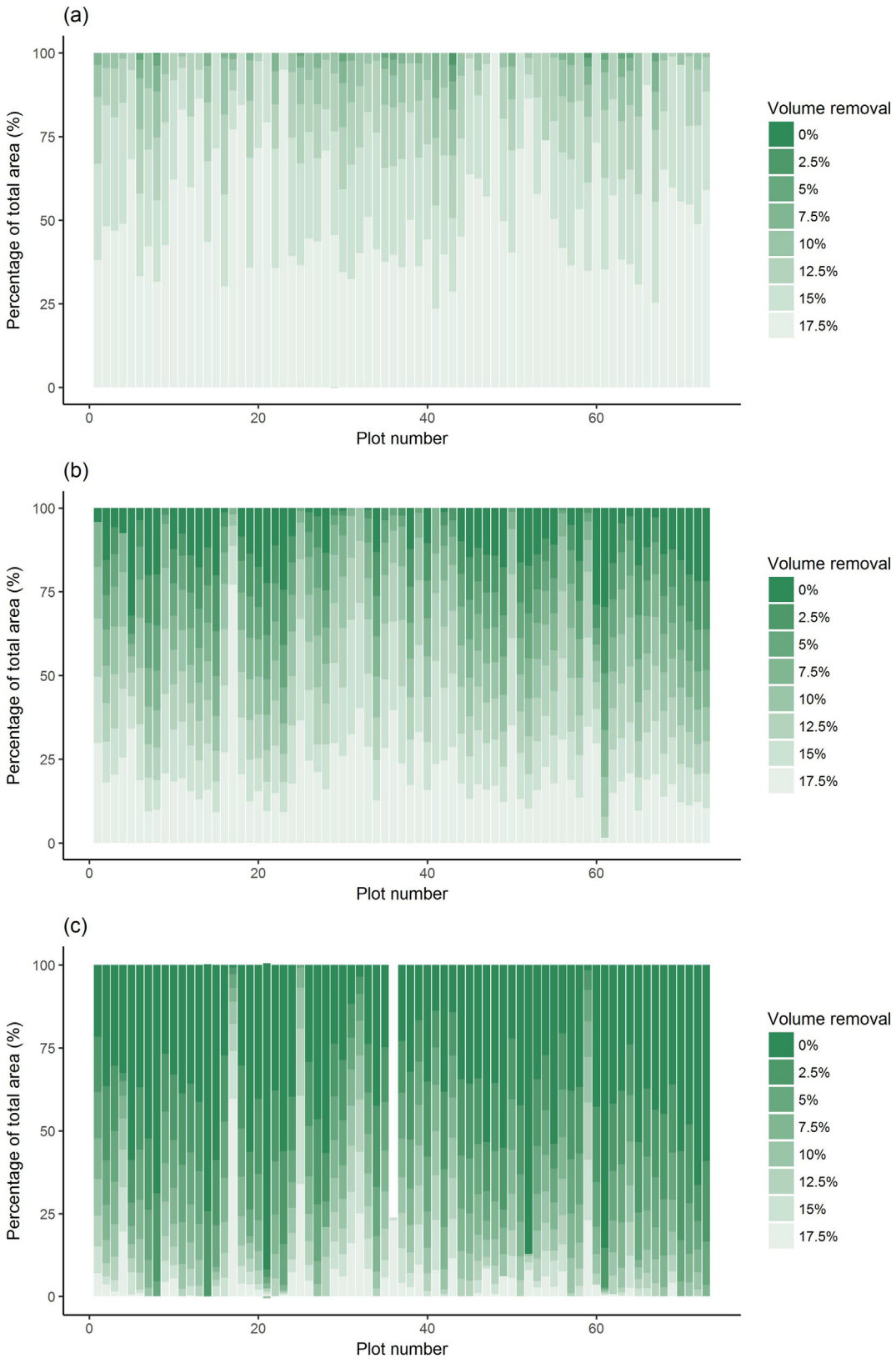

Fig. 6. Optimal management solution for maximizing bird abundance in each plot. The percentages indicate the area of each plot to be managed according to each management (% of volume removal). Fig. 6a considers bird abundance maximization with no TreMs requirements, Fig. 6b displays the optimal management considering 80% of TreMs maintenance and Fig. 6c shows the results for no TreMs loss (100% of maintenance).

could lead to a reduction of TreMs abundance in the next 50 years. A reduction in harvesting intensity can affect the profitability of harvesting operations. Nevertheless, due to the high standing stock ($405\ m^3 \cdot ha^{-1}$) and high wood price in the region ($84\ € \cdot m^{-3}$) harvesting operations can be profitable at a 10% harvesting level. Moreover, multifunctionality is the main goal of public forest administration, and the reduction of

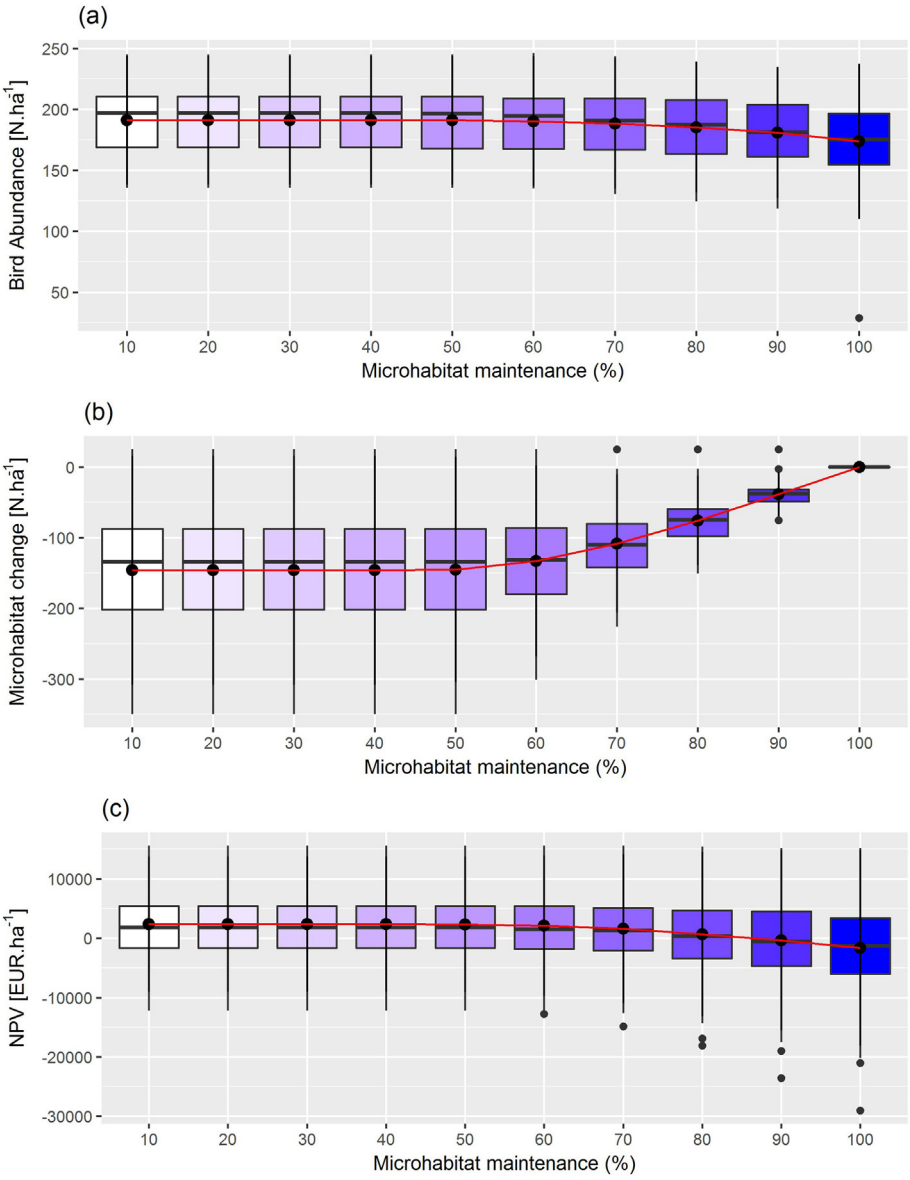

Fig. 7. Pareto frontier between bird abundance and microhabitat maintenance across all plots. Fig. 7a shows the maximum bird abundance with increasing levels of microhabitat maintenance. Fig. 7b displays the microhabitat loss and Fig. 7c shows the plots net present value (NPV) for the same tree microhabitat maintenance levels.

harvesting intensity is perceived to increase the value for other forest uses, such as recreation and carbon sequestration (Edwards et al., 2012; Yousefpour et al., 2018).

Our results suggest a set-aside area (no harvesting interventions) of around 10% restrict TreMs abundance loss to <20%. The national biodiversity strategy in Germany strives to increase the share of strict forest reserves to 5% of the total forest area by 2020 (Meyer et al., 2011). In state forests of Baden-Württemberg (and other German states), the target for strict forest reserves is 10% of the total area (ForstBW, 2015), which is compatible with our results.

4.5. Limitations

While forest birds are useful proxies for forest biodiversity and are currently employed as an indicator set for species richness and landscape quality in the monitoring report of the German Forest Biodiversity Strategy (BMUB, 2015), they might have different requirements than other taxa related to forest ecosystems (e.g. Paillet et al., 2010). Here, in addition to forest birds, we applied tree related microhabitats (TreMs) of living trees as a proxy for habitat requirements of other taxa. The restriction on TreMs to living trees limits our predictions to some extent, as TreMs of snags play an essential role for the forest biodiversity as well (Paillet et al., 2017). Nevertheless, our study is the first attempt to quantify future developments of TreMs and hence our results are valuable for management decisions, as management for timber production necessarily focuses on living trees. Moreover, extending the current analysis to include a larger set of species groups such as saproxylic organisms, ground vegetation and forest insects is needed to obtain a more complete picture of habitat requirements and to adjust conservation actions accordingly.

We did not consider tree species changes in our set of management options. Nevertheless, increasing tree species diversity is perceived as a suitable option to safeguard ecosystem functioning under climate change (Brunette et al., 2014) and increasing the share of broadleaf species in the landscape may benefit forest biodiversity (Seibold et al., 2015). Moreover, our analysis did not include the impact of forest disturbances on forest development. Disturbances are expected to interact with forest biodiversity, especially benefitting saproxylic organisms and negatively affecting profitability of forestry.

The impacts of climate change on the bird assemblage and TreMs was indirectly assessed, using altitude as a proxy for climatic suitability. The consideration of increasing temperature on metabolic rates, TreMs creation and species distribution is worth investigating. Additionally, the consideration of plant species range shifts may alter the bird and TreMs responses in the future. In this sense, coupling forest growth models with process-based community dynamics models and species range models may provide useful insight for planning conservation actions, regarding the extent and especially the optimal timing for their implementation.

5. Conclusions

Changing environmental conditions will affect forest and biodiversity dynamics in the future. It is crucial that the management of forest ecosystems takes into account these changes in forest biodiversity and promote its maintenance to sustain ecosystem functioning. Here we show that it will be necessary to apply a diversified set of management actions to promote forest biodiversity. This may include a decrease in harvesting intensity and an increase in the share of set aside areas as well as retention of habitat trees in production forests. These measures will help to maintain structural complexity including abundance and diverse tree-related microhabitats. However, it is clear that different taxa will respond differently to changing environmental conditions and management interventions. Therefore, we must strive to increase the complexity of forest landscapes, promoting biodiversity and enhancing ecosystem functioning, as well as its resistance and resilience in face of climate change.

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